Reward adaptation and the mechanisms of learning:

Contrast changes reward value in rats and drives learning.

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Abstract

Formal theories of learning suggest that associations between events are determined by the internal representations of those events. Thus learning should depend on perceived reward value – even when perceptions differ from objective values. We examined this prediction in flavour preference learning in rats. In two experiments, simultaneous contrast either increased perceived reward value - which was paired with distinctive flavour cue (the CS+); or decreased the perceived value of the same reward - which was then paired with a second flavour (the CS-). Even though the CS+ and CS- were paired with the same objective reward, there was a preference for the CS+ in subsequent tests. Moreover, the size of contrast-produced changes in reward value during training predicted the preference for the CS+ at test. This contrast-produced learning effect illustrates the mechanisms by which associations, which normally track veridical relationships between events in the world, are formed.

Keywords: Contrast Effects; Associative Learning; Flavour Preference; Comparative Psychology; Perceived Reward.

Consider two identical roast chicken dinners. Because they are the same meal, other things being equal, they should elicit the same response. Now imagine that one roast was eaten directly after a visit to a three Michelin star restaurant while the second was eaten directly after a somewhat ordinary cheeseburger. While the chicken dinner remains objectively the same, the contrast to the immediate prior experience means that it tastes far better after a dodgy burger than when compared to a finely crafted dining experience. Such contrast effects are ubiquitous across species and situations (Flaherty, 1996) and we have recently demonstrated that, as it does in humans (McBurney, 1972), the comparison of two different sucrose concentrations in rats appears to make the more concentrated one taste sweeter than it would otherwise while the less concentrated appears to taste less sweet than it would otherwise (Dwyer, Lydall, & Hayward, 2011).

Perhaps the simplest explanation of how contrast influences perception is adaptation of either sensory receptors or internal representations of stimuli. Responses to a stimulus reduce with extended exposure (Groves & Thompson, 1970; McBurney, 1972), so exposure to a highly concentrated solution will adapt the relevant receptors or internal representations thus leading to a lowered response when a weaker solution is encountered. Conversely, exposure to a weak solution will produce little adaptation, allowing a stronger response to subsequent stimulation. The effects of short-term adaptation on the internal representations of stimuli are well described by Wagner's SOP theory (1981).

The idea that contrast can change the internal representation of events is particularly intriguing because formal theories of associative learning – which account for how we and other animals learn about the relationships between stimuli and events in the world – are actually based on internal representations. The ability to learn that one event predicts another is vital in developing an appreciation of the regularity of relationships in the world (Dickinson, 2001). As a result, associative learning is functionally relevant because it tracks

the true contingencies between events. The analysis of the formation of links between the internal representations of events has been a mainstay of associative learning theory which applies across a vast range of situations and species: from human causal and social learning (Dickinson, 2001; Le Pelley et al., 2010) to food preferences and aversions (Garcia & Koelling, 1966; Logue, Ophir, & Strauss, 1981). One critical aspect of many learning accounts is that association formation is driven by how surprising a rewarding event is – in other words, the presence of an error between the expected outcome and what actually occurs (Rescorla & Wagner, 1972; Wagner, 1981).

Combining the concept of error-correction learning with the idea that sensory contrast changes the perception of stimuli (while obviously not affecting their objective properties) leads to the suggestion that contrast-dependant changes in reward processing should drive learning. That is, error correction learning, which is functionally important because it tracks the true contingencies between events, will be driven by the perception of reward value rather than the objective properties of the reward. Surprisingly, this proposition has yet to receive a direct empirical test.

Here, we report two flavour preference learning experiments in rats which examined whether contrast-produced changes in the perceived (but not actual) value of reward was sufficient to support learning, and more specifically, whether the size of any preference conditioned in this way was directly related to contrast-produced changes in the perception of rewards during training (as described in the discussion, a direct relationship is predicted by Wagner's SOP theory, 1981). While using contrast to investigate learning mechanisms might be novel, it is almost a truism that adaptation effects and other illusions are interesting partly because they illustrate the workings of perceptual mechanisms (Gregory, 1997; Mollon, 1974; Weiss, Simoncelli, & Adelson, 2002). Because learning and perception are typically so

functionally effective, it can be particularly informative to examine situations in which they depart from the objective situation.

*** Figure 1 about here ***

Experiment 1

The experiment used a contrast procedure in which exposure to 32% sucrose preceded 8% sucrose (mixed with a distinctive cue flavour – the CS-) on half of the training trials, and exposure to 2% sucrose preceded 8% sucrose (mixed with a distinctive cue flavour – the CS+) on the remaining trials (see Figure 1). As 8% sucrose should be perceived as more concentrated when following 2% sucrose than 32% sucrose, the CS+ is effectively (but not actually) being paired with a greater concentration of sucrose than the CS-. This should support a preference for the CS+ over the CS- when rats are subsequently choose between these cues alone. Moreover, the size of the contrast effect during training, which can be indexed by the average size of licking clusters (Dwyer, 2012; Dwyer et al., 2011 – see methods for a full description), should directly predict the size of the preference during test.

Methods

The full details of the methods can be found in the SOM-R. In brief, 14 male rats, with ad-lib access to food and water (which emphasises sensory rather than caloric effects of sucrose in flavour preference learning - Harris, Gorissen, Bailey, & Westbrook, 2000), were tested in a single cohort (two additional rats had been removed due to persistently low consumption: < 0.25ml/session). Because there was no prior literature available to estimate the effect size for contrast-produced learning, the sample size was chosen on the basis that 12 rats/group had been used in our prior study of contrast effects (see Experiment 2 of Dwyer et

al., 2011) and 16 rats were available prior to testing. Fluids were presented in drinking spouts that could be automatically advanced and retracted. The contrast stimuli were 2%, and 32% sucrose (w/w), while the cue solutions were 0.05% (w/w) grape and cherry Kool Aid flavours (Kraft Foods USA, Rye Brook, NY, USA) mixed with 8% sucrose (w/w).

Rats were trained with two types of trial in which a sample bottle was presented for 60s, which was then retracted and followed by presentation of a cue bottle for 60s: On CS+ trials the sample bottle contained 2% sucrose and the cue bottle the CS+ flavour mixed with 8% sucrose; on CS- trials the sample bottle contained 32% sucrose and the cue bottle the CS- flavour mixed with 8% sucrose (flavours were counterbalanced between grape and cherry). Rats received 16 CS+ and 16 CS- trials across eight days of training. The preference for the CS+ over the CS- flavour (both mixed with 8% sucrose) was then assessed in two 10-min preference tests in which the flavours were simultaneously available. There were also 1-bottle acceptance tests for the CS+ and CS- which are described in the SOM-R.

In order to assess the relative value of the solutions during training, a measure that is independent of consumption is needed. The detailed analysis of the microstructure of rats' licking behaviour reveals that they typically produce rhythmic sets of licks that can be grouped into clusters on the basis of the intervals between licks. The mean number of licks in a cluster (cluster size) is directly related to the concentration of palatable and unpalatable solutions independently of the amount consumed – with palatable solutions eliciting larger lick cluster sizes than unpalatable ones (for a review see, Dwyer, 2012; see also Davis & Smith, 1992; Spector, Klumpp, & Kaplan, 1998). These relationships imply that that lick cluster size provides an index of the perceived concentration and reward value of the solution being consumed. Thus, in addition to the consumption data, the mean cluster size was extracted. A cluster is defined as a set of licks each separated by an inter-lick-interval of no

more than 0.5s. Lick cluster data was not examined during 2-bottle preference tests as the opportunity to swap between bottles can interfere with the pattern of licking behaviour.

To examine how the size of the preference effect on test is related to the size of the contrast effect during training a single measure of each is required. A preference ratio for the CS+ during test was calculated as consumption of the CS+ divided by consumption of the CS+ and CS- added together. For this measure, values above 0.5 reflect a preference for the CS+, values below 0.5 reflect avoidance of the CS+ and values around 0.5 reflect indifference. Similar ratio measures were taken for all data reported here, for example lick cluster size for 8% sucrose after positive contrast divided by the sum of the lick cluster sizes for 8% sucrose after both positive and negative contrast was calculated as an index of the size of the contrast effect on reward value during training. These ratio measures were chosen because they are commonly used in studies of flavour preference conditioning (Ackroff, Touzani, Peets, & Sclafani, 2001; Dwyer, 2009; Sclafani & Ackroff, 1994).

*** Figure 2 about here ***

Results

Figure 2 shows the data for both the training (consumption and lick cluster size – see SOM-R for the sample bottle data) and test phases (consumption only) as mean values with 95% Confidence Intervals (CIs). The figure also shows the mean preference ratios (with CIs) for all measures. Looking first at the data from the cue bottles during training, consumption of 8% sucrose (with the CS+ flavour) on positive contrast trials was higher than consumption of 8% sucrose (with the CS- flavour) on negative contrast trials (Figure 2A), $t(13) = 4.24$, $p = .001$, SED = 0.13, Cohens's $d = 1.18$, and the lick cluster size was also higher on positive than negative contrast trials, $t(13) = 4.67$, $p < .001$, SED = 2.09, Cohens's $d = 1.25$ (Figure

2B). In addition, the CI for mean preference ratios for both consumption and lick cluster size for 8% sucrose following positive contrast did not include the indifference point of 0.5. Thus the addition of cue flavours did not prevent simultaneous contrast effects on either consumption or lick cluster size, and so these results confirm that our contrast-based manipulation of perceived reward value was successful.

Turning to the test, consumption of the CS+ was higher than that of the CS- during two-bottle tests, $t(13) = 2.82$, $p = .014$, SED = 0.71, Cohens's $d = 0.75$, and the preference ratio for CS+ consumption was higher than the indifference value of 0.5 and the CI did not include this value (Figure 2C). These results confirm that there was a preference for the CS+ solution. That is, pairing the CS+ with an 8% sucrose solution which had its reward value increased by positive contrast, created a preference for this CS+ solution when it was experienced without contrast (relative to the CS- solution which had been paired with an 8% sucrose solution which had its reward value decreased by negative contrast). In addition, it is clear from Figure 2D that the size of the preference displayed at test (indicated by the preference ratio for CS+ consumption) is directly related to the size of the contrast-produced change in reward value (indicated by the ratio of lick cluster sizes for 8% sucrose following positive and negative contrast in training). The CS+ preference at test was correlated with the contrast produced change in reward value in training as indicated by lick cluster size, $r(14) = .64$, $p = .013$ [95% CI = .17 – .87] (a partial correlation which controlled for differences in consumption of the CS+ and CS- during training was also significant, $r(11) = .60$, $p = .030$ [95% CI = .10 – .86]). Moreover, CS+ preference at test was not correlated with the relative consumption of the CS+ and CS- during training, $r(14) = .35$, $p = .224$ [95% CI = -.23 – .74].

Discussion – Experiment 1

The results of Experiment 1 were entirely in line with the prediction that contrast-produced changes in the value of sucrose should drive preference learning. While it is true that the CS solutions are experienced following either 32% or 2% sucrose and thus might be subject to contrast themselves, and more of the CS+ solution is consumed than of the CS- solution during training, it is highly unlikely that either of these contributed to the observed preference for the CS+ over the CS- at test. Firstly, adaptation to one solution has no effect on the perceived reward value (indexed by lick cluster size) of one with different sensory properties (Dwyer et al., 2011) suggesting that contrast is unlikely to directly affect the sensory processing of the CSs. Moreover, rats prefer flavours that are consumed when replete over other flavours (Capaldi & Myers, 1982; Capaldi, Myers, Campbell, & Sheffer, 1983) and the CS- flavour was consumed alongside the highly satiating 32% sucrose. This also reinforces the idea that the results are driven by sensory processing of reward solution rather than caloric/motivational effects because the CS- and not the CS+ is presented in the context of larger caloric load. In addition, neophobia aside, differences in consumption alone do not produce reliable preferences (Fanselow & Birk, 1982) and the preference effects at test were not correlated with consumption differences in training.

We nevertheless performed an additional experiment to both replicate the basic effect and also to directly rule out these possible confounds. Thus Experiment 2 (Figure 1) used fructose (which supports preferences on the basis of its palatable flavour and not caloric content - Ackroff et al., 2001; Sclafani & Ackroff, 1994) in the place of sucrose and a control condition was added whereby consumption was capped to reduce differences in the consumption of the CS+ and CS- during training.

Experiment 2

Methods

The methods of Experiment 2 were as in Experiment 1, with the exception that fructose replaced sucrose and 24 rats were used in a single cohort. The sample size was chosen on the basis that 12 rats/group had been used in our prior study of contrast effects with sucrose (see Experiment 2 of Dwyer et al., 2011) and Experiment 1 had shown very distinct contrast-produced learning with an effective sample size of 14. The procedure was identical to that of Experiment 1 for half of the rats (Group Free Access) other than the use of fructose. The remaining rats (Group Restricted) received the same general procedures with the exception that drinking from the cue bottle during training was limited to a maximum of 75 licks per trial thus reducing differences between CS+ and CS- consumption.

*** Figure 3 about here ***

Results

Figure 3 shows the data for both the training (consumption and lick cluster size – see SOM-R for the sample bottle data) and test phases (consumption only) as mean values with 95% Confidence Intervals (CIs). When animals were allowed free consumption, both consumption and lick cluster size were higher for 8% fructose when it followed 2% fructose than when following 32% fructose (Figure 3A/3B). When restricted to 75 licks per cue bottle trial consumption of 8% fructose was similar between the positive and negative contrast conditions, however the difference in lick cluster size remained (Figure 3A/3B). Thus simultaneous contrast effects are present with fructose as the rewarding solution, and the effects of contrast on lick cluster size do not depend on the presence of large differences in consumption.

Analysis of consumption from the cue bottles using a mixed ANOVA with a within-subject factor of sample concentration (2% vs. 32%) and a between subject factor of

restriction status (free vs. restricted) revealed main effects of sample concentration, $F(1,22) = 58.42$, $p < .001$, MSE = 0.271, $\eta^2 = .50$, and restriction, $F(1,22) = 35.56$, $p < .001$, MSE = 0.506, $\eta^2 = .62$, as well as a significant interaction between restriction and sample concentration, $F(1,22) = 37.30$, $p < .001$, MSE = 0.271, $\eta^2 = .32$. Simple effects analyses showed that the difference in consumption of 8% fructose when it followed 2% and 32% fructose was significant in the free access group, $F(1,22) = 94.53$, $p < .001$, MSE = 0.045, $\eta^2 = .81$, but not in the restricted access group, $F(1,22) = 1.179$, $p = .289$, MSE = 0.045, $\eta^2 = .05$. For lick cluster size, there was a main effect of sample bottle concentration, $F(1,22) = 71.66$, $p < .001$, MSE = 54.25, $\eta^2 = .76$, but no main effect of restriction or interaction between these factors, Fs < 1. In addition, for the free consumption group, the CI for mean preference ratios for both consumption and lick cluster size for 8% fructose following positive contrast did not include the indifference point of 0.5. For the restricted consumption group, although the mean preference ratio for consumption of 8% fructose following positive contrast was lower than that in the free consumption group, the CI did not include the indifference point of 0.5, suggesting that restriction had not totally equated consumption of the CS+ and CS-. For the restricted consumption group the CI for mean preference ratio for lick cluster size for 8% fructose following positive contrast did not include the indifference point of 0.5 (and the mean preference ratios for the free and restricted groups were similar with an almost total overlap between the respective CIs).

Turning to the critical test data, consumption of the CS+ was higher than that of the CS- regardless of restriction during the training phase (Figure 3C). A mixed ANOVA with a within-subject factor of cue type (CS+ vs. CS-) and a between subject factor of restriction status (free vs. restricted) revealed a main effect of cue type, $F(1,22) = 23.37$, $p < .001$, MSE = 5.27, $\eta^2 = .52$, but no main effect of restriction or interaction between these factors, Fs < 1. In addition, the mean preference ratios for the CS+ in the free and restricted groups were

nearly identical and there was an almost total overlap between the respective CIs (which both fell entirely above the indifference point of 0.5). In short, a CS+ flavour that had previously been presented with 8% fructose that was subject to positive contrast was preferred to a CS- flavour that had previously been presented with 8% fructose that was subject to negative contrast when both flavours were simultaneously available. These effects were not influenced by restricting consumption of the CS+ and CS- flavours during training.

Inspection of Figure 3D reveals that, for both free and restricted consumption groups, the size of the preference displayed at test (indicated by the preference ratio for CS+ consumption) is directly related to the size of the contrast-produced change in reward value (indicated by the ratio of lick cluster sizes for 8% fructose following positive and negative contrast in training). For the free access group, $r(12) = .59$, $p = .044$ [95% CI = .02 – .87] (a partial correlation which controlled for differences in consumption of the CS+ and CS- during training was also significant, $r(9) = .61$, $p = .045$ [95% CI = .05 – .88]) and the restricted access group, $r(12) = .58$, $p = .049$ [95% CI = .01 – .87] (a partial correlation which controlled for differences in consumption of the CS+ and CS- during training was also significant, $r(9) = .61$, $p = .048$ [95% CI = .06 – .88]). As in Experiment 1, there was no correlation between CS+ preference at test and variations in the relative consumption of the CS+ and CS- during training for either the free consumption group, $r(12) = .24$, $p = .457$ [95% CI = -.39 – .72], and restricted consumption group, $r(12) = -.03$, $p = .901$ [95% CI = -.68 – .45].

Table 1- Meta-analysis of 3 experimental sub groups

	Measure	Consumption	Lick cluster size
Training Cue Bottle	Ratio (Positive Contrast / Total)	0.65 [0.62 – 0.68]	0.62 [0.60 – 0.64]
2-bottle Test	Ratio (CS+ / Total)	0.68 [0.62 – 0.75]	

Note: Data is shown as mean [with 95% CI].

While the results in Experiments 1 and 2 are clear, the precision of the estimates is relatively low. Thus we performed a meta-analysis combining the three experimental groups reported here (i.e. Experiment 1, and the free and restricted consumption groups from Experiment 2). This focused on the behavioural measures that were most critical for the hypotheses under test: the ratio between lick cluster size for the reward (8% sucrose or fructose) following positive and negative contrast in training; the ratio between consumption of the CS+ and CS- in training; the ratio between consumption of the CS+ and CS- at test (all these are shown in Table 1); the correlation between the size of the CS+ preference at test and the size of the contrast effect in training; and the correlation between the size of the CS+ preference at test and the relative consumption of the CS+ over the CS- at training. Analysis of the mean ratio data used the Exploratory Software for Confidence Intervals (ESCI, Cumming, 2013) and correlations used the SPPS syntax provided by Field and Gillet (2010), using fixed-effects models in both cases. The combined estimates (see Table 1) of the preference ratios for both CS+ consumption and lick cluster size for the reward in training are well above the indifference point of 0.5, confirming the reliability of the contrast-based manipulation of reward value. Moreover, the combined estimate of the preference for the CS+ at test also falls well above the indifference value of 0.5, indicating that this contrast-produced preference for the CS+ was reliable.

Perhaps most importantly, the combined estimate of the correlation between the CS+ preference at test with the contrast produced change in reward value in training was .61 [95% CI = .33 – .79], and for the correlation between the CS+ preference at test and the relative CS+/CS- consumption in training was .20 [95% CI = -.16 – .51]. The difference between these two correlations is .41 [95% CI =.02 – .79], confirming that contrast produced changes in reward value are a better predictor of the acquired CS+ preference than the amount of training consumption.

General Discussion

Changes in the perceived, but not actual, value of a rewarding solution produced by contrast effects were sufficient to support new flavour preference learning in rats. Moreover, the size of the acquired preference was directly related to the size of the contrast effect in training. The fact that animals learn based on subjective experience rather than objective stimulus properties is a timely reminder that the functional outcome of behaviour (e.g. tracking contingencies between events in the world) does not provide a direct guide to the mechanisms involved in its production. Although the details of formal theories of associative learning such as Wagner's SOP theory (1981) may seem a matter for the aficionado, the results we have obtained here are directly in accordance with the predictions of that theory (the SOM-R contains a detailed derivation of this prediction).

In setting out SOP, Wagner (1981) was careful to describe how it accounted for the fact that exposure to a reward would both reduce the response to subsequent experience of that reward (Pfautz, 1980, as cited in Wagner, 1981) as well as the degree of learning supported by that subsequent reward (Domjan & Best, 1977; Terry, 1976). While SOP does indeed account for both the effects of reward exposure on responding to the reward and on its ability to support learning, the truly critical aspect of Wagner's account is that these two

effects should be inextricably linked because they both rely on the same mechanism. However, no previous study has concurrently examined the effects of reward exposure on both responding to the reward and on learning supported by that reward.

Although Wagner himself never analysed contrast effects within the SOP framework, it provides a direct account of the effects on contrast on licking microstructure (Dwyer et al., 2011). Therefore, the experiments presented here, examining the relationship between lick cluster size in training (i.e. a measure of reward exposure on the response to the reward) and the degree of preference at test (i.e. a measure of reward exposure on learning supported by the reward), provide the first direct test of SOP's prediction that reward exposure effects on learning and unconditioned responses should be directly related. The fact that exactly this relationship between contrast-produced adaptation and preference learning was observed in the current experiments demonstrates that Wager's SOP theory accurately characterizes the manner in which internal representations of events are processed and associated.

While the change in the rewarding value of sucrose produced by contrast has thus far been considered in terms of perceptual changes, the idea that "value" is inherently relative is widespread (for a review see Vlaev, Chater, Stewart, & Brown, 2011). Vlaev et al. (2011) make a critical distinction between "relative evaluation" models (e.g. Tversky & Simonson, 1993) which compute the value of options relative to the context in which they appear, and "purely comparative" models (e.g. decision by sampling, Stewart, Chater, & Brown, 2006) which discard the notion of value entirely and propose that choices can be explained entirely by comparisons between options.

Despite their differences, both classes of model might apply to the current situation to some degree. Considering first the idea of relative evaluation: In our experiments each flavour is experienced in the training phase in the context of one other sugar solution – thus the value of that flavour will be enhanced when the context contains an alternative of lower

value, and decreased when the context contains an alternative of higher value. This can explain the different values of the flavours during the training phase, but at test, the local context no longer contains any different comparators, and the background context includes exposure to both high and low value alternatives. Thus the current results suggest an additional consideration for relative evaluation models – namely that relative value is "cached" and recalled at when options are offered in a new context.

Turning to the idea of pure comparison: The decision by sampling model assumes that choice is determined by comparison to both currently available options, and to options retrieved from memory. Again, a simple application of this model has difficulty in explaining the current test results because the rats would have experienced lower and higher value options than the two choice flavours equally often, and the fact that the choice flavours are both intermediate between these should lead to a convergence between them. Thus the current results suggest an additional consideration for decision by sampling – namely that in choice situations the memories retrieved by each individual option will be more highly weighted in the comparisons made for that option than for others that are concurrently available. To take a broader perspective, in reviewing the different comparative theories of choice, Vlaev et al. (2011) ask whether they are best conceived as lying at functional, algorithmic, or mechanistic levels. One possible integration of the theoretical ideas considered here is that associative learning theories such as Wagner's SOP model (1981) could provide a (partial) mechanistic level account for the functional relationships identified by choice theories.

In summary, flavour preference learning in rats was sensitive to perceived relationships between events rather than the objective properties of the stimuli. This relationship is entirely in accordance with the predictions of a formal model of associative learning (Wagner, 1981). Just as adaptation effects and visual illusions reveal the workings of

perceptual systems, the current contrast learning effect informs us about the mechanisms by which associations, which normally track the real relationships between events in the world, are formed.

Author Contributions

DMD developed the study concept. DMD and JF designed Experiment 1, while DMD, PG, and ML designed Experiment 2. Testing was performed by JF and PG. DMD performed the data analysis and drafted the original manuscript, all other authors provided critical revisions. All authors approved the final version of the manuscript.

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Figure Captions

Figure 1. A – Illustrates the basic contrast effect and general design. The perceived palatability/concentration of 8% sucrose is enhanced when encountered immediately after 2% sucrose (positive contrast), and diminished when encountered immediately after 32% sucrose (negative contrast). Here, one flavour (the CS+) is mixed with 8% sucrose when subject to positive contrast, and a second flavour (the CS-) is mixed with 8% sucrose when subject to negative contrast, prior to testing the preference for the CS+ vs the CS- in the absence of contrast. B – Gives the full experimental design. Each training session consisted of four trials, each comprising 60s access to the sample bottle then 60s access to the cue bottle, followed by a 300s inter-trial interval with no fluid access. All four trials in a session were in the same

condition and there were four sessions per condition. CS+ and CS- flavours were counterbalanced between 0.05% grape and cherry Kool Aid. During the test phase, consumption of the CS+ and CS- flavours was examined in two-bottle preference tests in which both flavours were simultaneously available.

Figure 2. Experiment 1: A – Mean training consumption (g), with 95% CI, from the cue bottles. Numbers above the bars show the mean preference ratio (with 95% CI). B – Mean training lick cluster size, with 95% CI, from the cue bottles. Numbers above the bars show the mean preference ratio (with 95% CI). C – Mean 2-bottle test consumption (g), with 95% CI, of the CS+ and CS- flavours in the absence of contrast. Numbers above the bars show the mean preference ratio (with 95% CI). D – Scatterplot of preference ratio for the CS+ at test against the ratio of lick cluster sizes (LCS) for 8% sucrose following positive and negative contrast in training. The trend line represents the linear correlation.

Figure 3. Experiment 2: A – Mean training consumption (g), with 95% CIs, from the cue bottles for both free and restricted consumption groups. Numbers above the bars show the mean preference ratio (with 95% CIs). B – Mean training lick cluster size, with 95% CIs, from the cue bottles for both free and restricted consumption groups. Numbers above the bars show the mean preference ratio (with 95% CIs). C – Mean 2-bottle test consumption (g), with 95% CIs, of the CS+ and CS- flavours in the absence of contrast for both free and restricted consumption groups. Numbers above the bars show the mean preference ratio (with 95% CI). D – Scatterplot of the preference ratio for the CS+ at test against the ratio of lick cluster sizes (LCS) for 8% sucrose following positive and negative contrast in training for both free and restricted consumption groups. The trend lines represent the linear correlations.

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Figure 1

A – General Procedure

Positive Contrast: 2% sucrose → 8% sucrose & Flavour 1 (CS+?)

Negative Contrast: 32% sucrose → 8% sucrose & Flavour 2 (CS-?)

Current experiments ask if Flavour 1 (paired with 8% sucrose positively revalued by contrast to 2% sucrose) will be preferred to Flavour 2 (paired with 8% sucrose negatively revalued by contrast to 32% sucrose).

B – Design Table

	Condition	Sample Bottle	Cue Bottle	Test
Experiment 1				
	Positive Contrast	2% sucrose	CS+ & 8% sucrose	CS+ vs. CS- (both with 8% sucrose)
	Negative Contrast	32% sucrose	CS- & 8% sucrose	
Experiment 2				
Free	Positive Contrast	2% fructose	CS+ & 8% fructose	
	Negative Contrast	32% fructose	CS- & 8% fructose	
Restricted	Positive Contrast	2% fructose	CS+ & 8% fructose (maximum 75 licks per trial)	CS+ vs. CS- (both with 8% fructose)
	Negative Contrast	32% fructose	CS- & 8% fructose (maximum 75 licks per trial)	

Figure 2

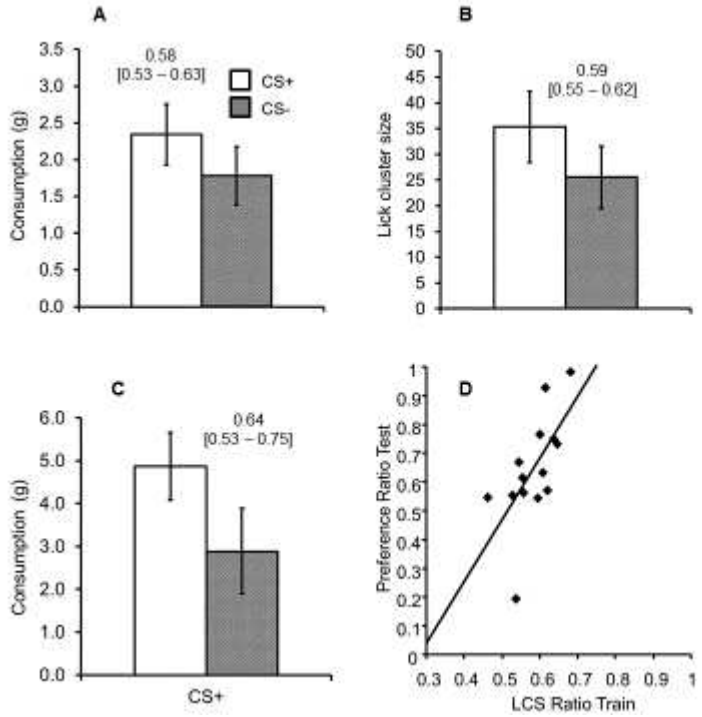
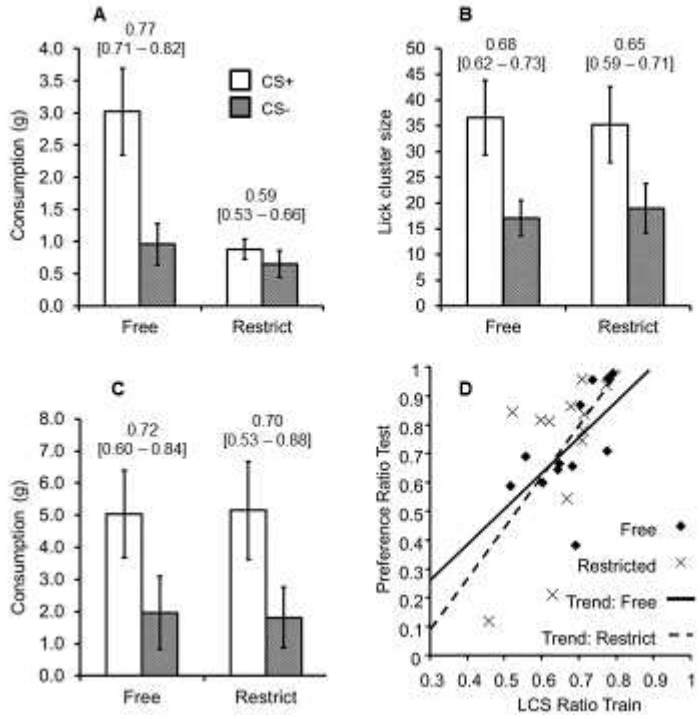


Figure 3


A
0.77
[0.71 – 0.82]
CS+
CS-
0.59
[0.53 – 0.66]
Consumption (g)
Free
Restrict
B
0.68
[0.62 – 0.73]
0.65
[0.59 – 0.71]
Lick cluster size
Free
Restrict
C
0.72
[0.60 – 0.84]
0.70
[0.53 – 0.88]
Consumption (g)
Free
Restrict
D
Preference Ratio Test
LCS Ratio Train
Free
Restricted
Trend: Free
Trend: Restrict